Growth of Tree Seedlings As Affected by Light Intensity

V. White Ash, Beech, Eastern Hemlock, and General Conclusions

by

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ABSTRACT

White ash (*Fraxinus americana* L.), beech (*Fagus grandifolia* Ehrh.), and eastern hemlock (*Tsuga canadensis* (L.) Carr.) were grown for 7 years in 13, 25, 45, and 100% of full light. Growth was measured in terms of height and dry weight. Although seedlings growing in 13% light were at least as tall as those in full light, maximum dry matter was produced in 45% light. It is concluded that, of the four light intensities studied, 45% is the optimum for these three species.

With the conclusion of this series of studies, two of the attributes ascribed to tolerant and intolerant trees are examined with reference to the data obtained. The findings support the statements that the ability to maintain good root growth increases with an increasing degree of tolerance, and that tolerant species have inherently low growth rates.

RÉSUMÉ

Le Frêne blanc (*Fraxinus americana* L.), le Hêtre américain (*Fagus grandifolia* Ehrh.) et la Pruche (*Tsuga canadensis* (L.) Carr.) crûrent durant 7 ans sous 13, 25, 45 et 100% de pleine lumière. La croissance était mesurée en termes de hauteur et de poids de matière anhydre. Les semis sous 13% de lumière étaient aussi grands que ceux qui furent soumis à la pleine lumière mais cependant ceux qui contenaient le maximum de matière anhydre avaient été soumis à 45% de lumière. On peut conclure que des quatre chiffres choisis, ce dernier constitue l'optimal pour les trois espèces.

Avec la fin de cette série d'études, l'auteur interprète les résultats obtenus en rapport avec deux des attributs des arbres tolérant ou ne tolérant pas l'ombre. Il conclut que la capacité de maintenir une bonne croissance des racines augmente avec le degré de tolérance de l'espèce pour l'ombre, et que les espèces tolérantes possèdent de façon inhérente un taux réduit de croissance.

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INTRODUCTION

This is the last in a series of reports on the effect of light intensity on the growth of tree seedlings. The purpose of the research was to describe the height and dry weight of 22 species of native-tree seedlings grown in four light intensities and thus to obtain broad prescriptions of optimum light requirements for regeneration. This study, unlike most of its kind, permits valid comparisons between many species because all grew simultaneously at one location. The series also describes the light requirements of a number of species not previously reported on.

Fourteen species native to eastern Canada were dealt with in earlier reports (Logan, 1965, 1966, 1966a, 1969). This report describes the effect of light intensity on the growth of three shade-tolerant species - white ash (*Fraxinus americana* L.), beech (*Fagus grandifolia* Ehrh.), and eastern hemlock (*Tsuga canadensis* (L.) Carr.). The five remaining species were damaged during the experiment and had to be abandoned.

METHOD

Forty seedlings of each species were grown in an open area (100% light) and in lath and fiber-glass shelters that admitted 13, 25, and 45% of full light. Light was measured on clear sunny days with spherical illuminometers having a spectral response similar to that of the human eye. Shelters were found to have a relatively small effect on air temperature and on evaporation from Piché atmometers (Logan, 1965). To maintain adequate moisture in all treatments, seedlings were watered during dry weather. It was concluded that in this experiment treatments varied mainly in light. Further details on methods, environmental measurements, and soil are given elsewhere (Logan, 1965, 1966a).

Height, leaf dimensions, and diameter at the root collar were measured annually. Data presented in this report are means of 10 seedlings per species that were retained to the end of the experiment.

Root growth was measured on a sample of 4-year-old beech and 7-year-old hemlock. For this purpose, 10 seedlings of average size were selected from each treatment and dry weights (105 C) of roots were determined. Removal of these samples did not alter the height distribution of the remaining stems. At 7 years of age shoot dry weights for all three species were obtained from samples of 10 seedlings. Leaf area per seedling was calculated by obtaining a weight-per-unit-area factor from a small sample of leaves from each treatment and applying this factor to the total weight of foliage per seedling. The significance of differences between means ($P = .05$) was determined by "t" tests.

RESULTS

Between 3 and 7 years of age, the three species in this study were taller when grown in shade than when grown in full light (Table 1 and Figure 1). For 7-year-old white ash and hemlock the differences between 13% light and full light were not significant, whereas beech seedlings in all three shade treatments were significantly taller than those in full light.

Leaves of white ash and beech were larger on the seedlings grown in shade than on those grown in full light (Table 2). Hemlock needles were the same length (0.4 inch) regardless of light treatment. Leaf areas calculated for white ash and beech increased with increasing light to a maximum in 45% light and then declined for seedlings grown in full light (Table 3).

Seedlings grown in 13% light had smaller diameters at the root collar than those in other shade treatments, but there was little difference in the diameters of seedlings grown in 25%, 45%, or full light (Table 4).

TABLE 1. AVERAGE HEIGHT (IN INCHES) OF SEEDLINGS GROWN IN FOUR LIGHT INTENSITIES FOR 7 YEARS

Species	13%	25%	45%	100%
White ash	59^{ab}	66^{bc}	73^{c}	50^{a}
Beech	46^{a}	47^{a}	45^{a}	31
Eastern hemlock	17^{a}	23^{b}	26^{b}	14^{a}

Note: Common letters denote treatments in which a species showed no significant differences in height. Means based on 10 seedlings.

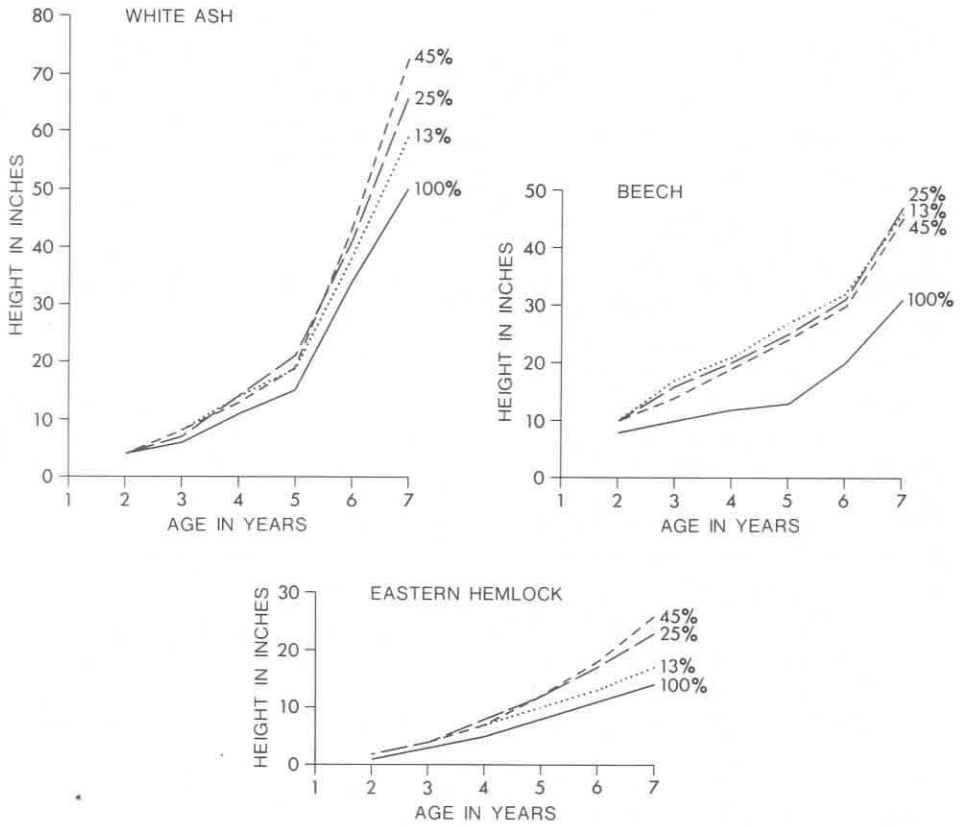


Figure 1. Average height of white ash, beech, and eastern hemlock seedlings growing in 13, 25, 45, and 100% of full light, age 2 to 7 years.

TABLE 2. AVERAGE DIMENSIONS (IN INCHES) OF WHITE ASH LEAFLETS AND BEECH LEAVES FROM SEEDLINGS GROWN IN FOUR LIGHT INTENSITIES FOR 7 YEARS

Species	13%		25%		45%		100%	
	Length	Width	Length	Width	Length	Width	Length	Width
White ash	4.4	2.2	4.5	2.3	4.0	2.0	3.0	1.4
Beech	4.5	2.3	4.5	2.3	4.5	2.2	3.9	2.0

Note: Means based on a typical leaf from each of 10 seedlings.

TABLE 3. CALCULATED LEAF AREA (DM^2) OF WHITE ASH AND BEECH SEEDLINGS GROWN IN FOUR LIGHT INTENSITIES FOR 7 YEARS

Species	13%	25%	45%	100%
White ash	86^{a}	110	166	85^{a}
Beech	62^{a}	94^{bc}	107^{c}	77^{ab}

Note: Common letters denote treatments in which a species showed no significant differences in leaf area. See text for method of calculation.

TABLE 4. AVERAGE ROOT-COLLAR DIAMETER (IN MILLIMETERS) OF SEEDLINGS GROWN IN FOUR LIGHT INTENSITIES FOR 7 YEARS

Species	13%	25%	45%	100%
White ash	17	21^{a}	24	20^{a}
Beech	16	18^{a}	21^{b}	20^{ab}
Eastern hemlock	5	8^{a}	10^{b}	8^{ab}

Note: Common letters denote treatments in which a species showed no significant differences in root-collar diameter.

Table 5 shows the distribution of dry matter between foliage, branch, and main stem. Maximum weights of above-ground parts were usually found on seedlings grown in 45% light, and minimum weights on seedlings grown in 13% light. Differences in seedling weights between 25% and full light were generally not significant.

Dry weights of roots of 4-year-old beech and 7-year-old hemlock are given in Table 6 (see also Figure 2). No root weights are available for white ash. Root weights, like the weights of shoots, reached a maximum on seedlings grown in 45% light.

TABLE 5. DRY WEIGHT (IN GRAMS) OF FOLIAGE, BRANCH, MAIN STEM, AND TOTAL SHOOT OF SEEDLINGS GROWN IN FOUR LIGHT INTENSITIES FOR 7 YEARS

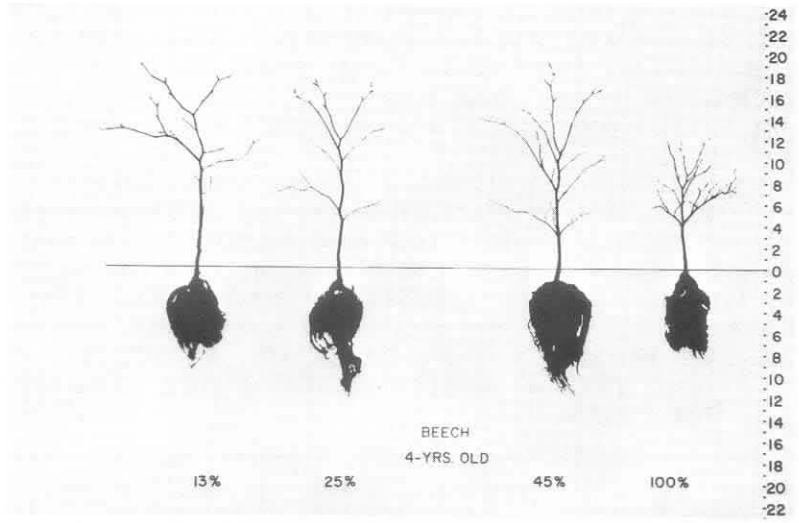
Category	Species	13%	25%	45%	100%
Foliage	White ash	32	54[a]	93	64[a]
	Beech	19	32[a]	45[b]	38[ab]
	Eastern hemlock	6	14[a]	22	12[a]
Branch	White ash	12[a]	15[a]	59	36
	Beech	28	52[a]	75[a]	52[a]
	Eastern hemlock	2	7[a]	11	6[a]
Stem	White ash	74[a]	116	163	80[a]
	Beech	47[a]	69	90	55[a]
	Eastern hemlock	2	4[a]	6[a]	3
Total shoot	White ash	118	185[a]	315	180[a]
	Beech	94	153[a]	210	145[a]
	Eastern hemlock	10	25[a]	39	21[a]

Note: Common letters denote treatments in which a species showed no significant differences in weight.

TABLE 6. OVEN-DRY ROOT WEIGHT (IN GRAMS) OF 4-YEAR-OLD BEECH AND 7-YEAR-OLD EASTERN HEMLOCK GROWN IN FOUR LIGHT INTENSITIES

Species	13%	25%	45%	100%
Beech	10[a]	12	17	7[a]
Eastern hemlock	6	19[a]	31	20[a]

Note: Common letters denote treatments in which a species showed no significant differences in root weight.



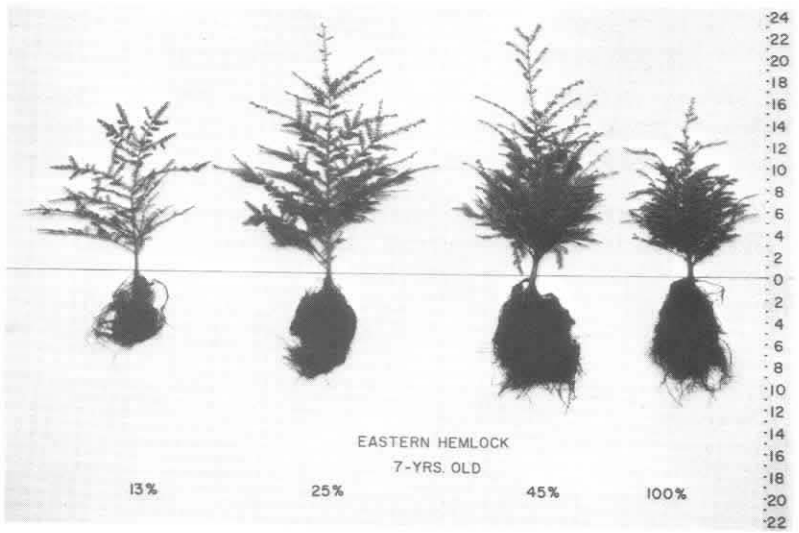


Figure 2. Four-year-old beech and 7-year-old hemlock of average size grown in 13, 25, 45, and 100% of full light. The numbers on the right represent inches.

DISCUSSION

White Ash

Most of the parameters measured - height, root-collar diameter, dry weight of foliage, branch, and main stem - reached maximum values when seedlings were grown in 45% light. Of the light intensities studied in this report, this has clearly been the most favorable for the growth of white ash seedlings. In 45% light, white ash developed a good branch system (Table 5) with maximum leaf area, which could account in part for its good growth under this treatment.

In 13% light, height and weight of the main stem of white ash seedlings were comparable to those of seedlings grown in full light. On this basis, white ash seedlings could be rated as tolerant of shade. Wright (1959) points out that young seedlings are "shade-enduring" but become more intolerant with increasing age. Thus Baker (1950) lists this species as intermediate in his table of five tolerance classes.

Beech

The height growth of beech was unaffected by an increase from 13 to 45% of full light, whereas the dry-matter production of root and shoot increased to a maximum in 45% light. When light was increased from 45% to full light, leaf area declined and height, root weight, and shoot weight were reduced. These results indicate that 45% is the optimum light intensity tested for the growth of beech seedlings.

When beech was grown in 13% light, its decline in height and dry weight from the maximum values obtained was less than that of white ash, and on this basis beech is judged to be more tolerant of shade than white ash. Rushmore (1961) reports that beech seedlings develop better under moderate canopy than in open areas, and the present study bears this out. Beech seedlings grown in shade were considerably taller than those grown in full light, and stem and root weight of seedlings in 13% light were the equivalent of those in full light. Sugar maple (*Acer saccharum* Marsh.) was the only other species studied in this series that attained the same height in all shade treatments (Logan, 1965), and Baker (1950) rates both sugar maple and beech as very tolerant.

Eastern Hemlock

Eastern hemlock seedlings also reached their maximum dry-matter production when grown in 45% light. The drop in foliage production in full light may have contributed to the decline in

growth under that treatment. The shade tolerance of hemlock is apparent when seedlings grown in shade are compared in both height and weight with those grown in full light. Hough (1960) states that establishment of hemlock seedlings is better in shade than in full sun. Subsequent growth, as shown in this study, is also better in partial shade.

One other tolerant conifer, balsam fir (*Abies balsamea* (L.) Mill.), was studied in this series. The relative reductions in height and dry weight of seedlings grown in 13% light show that eastern hemlock is more shade-tolerant than balsam fir.

GENERAL CONCLUSIONS

With the conclusion of this series of studies on the effect of light intensity on the growth of tree seedlings, two of the attributes ascribed to tolerant and intolerant species can be re-examined.

Bates (1925) and Bates and Roeser (1928) suggested that tolerant species maintain good root growth when grown in low light. This was disputed by Shirley (1943) and Baker (1945), who found little correlation between root development and degree of tolerance. In Table 7, root development in low light is measured by comparing root weights of seedlings grown in 13% light with those of seedlings grown in full light. This criterion shows that, with the exception of three of the conifers, the ability to maintain good root growth in low light does increase with increasing tolerance. But only the very tolerant species show appreciable root growth in low light.

The second concept to be examined here is that tolerant trees have inherently low growth rates and are capable of maintaining life at a low metabolic level, whereas intolerant trees have an inherently rapid growth rate in full light but cannot adapt to low light, which restricts their growth (Toumey and Korstian, 1947; Baker, 1950; Went, 1957). Baker (1950) suggests that intolerant species may starve themselves in low light by their rapid growth rate. According to Went (1957), the ability to adapt to shade may have arisen through selection for low rates of respiration and photosynthesis and hence for low growth rates in all environments. This is supported by Grime (1965), who found that tolerant trees had lower relative growth rates and lower respiration rates than intolerant species.

The data obtained in this series of papers support the contention that tolerant trees have inherently low growth rates. Results for the groups of species studied are summarized in Figure 3, which shows the maximum shoot dry weight of each species relative to the shoot dry weight of the largest species in the group. The trend toward less growth with increasing tolerance is evident.

TABLE 7. ROOT WEIGHT OF SEEDLINGS GROWN IN 13% LIGHT COMPARED WITH THAT OF SEEDLINGS GROWN IN 100% LIGHT FOR TREE SPECIES STUDIED IN THIS SERIES

Tolerance class	Hardwood species	Root wt 13% / Root wt 100%	Age	Coniferous species	Root wt 13% / Root wt 100%	Age
Very intolerant				Jack pine	0.03	4
				Larch	0.05	4
Intolerant	White birch	0.26	3	Red pine	0.04	4
Intermediate	Yellow birch	0.29	3	White pine	0.06	4
	White elm	0.33	3			
	White ash	no data				
Tolerant	Silver maple	0.37	3	Black spruce	0.02	4
	Basswood	0.36	4	White spruce	0.09	4
				Eastern white cedar	0.01	4
Very tolerant	Sugar maple	0.87	3	Balsam fir	0.17	4
	Beech	1.43	4	Eastern hemlock	0.30	7

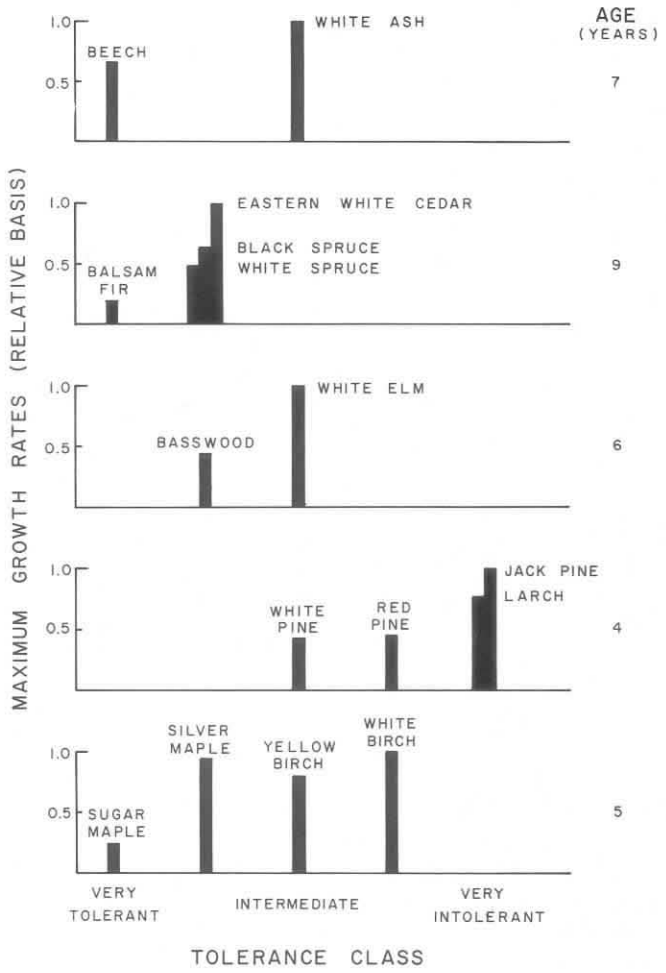


Figure 3. Maximum shoot dry weight of each species relative to the maximum shoot dry weight of the largest species in the group. The groups correspond to those appearing in earlier reports in this series.

The inability of intolerant trees to adapt to low light can be measured by comparing the shoot weight of seedlings grown in 13% light with that of seedlings grown in full light (Table 8). This attribute is poorly correlated with tolerance. This study shows that low light severely restricts the growth of all conifers except the two very tolerant species. Shade affects hardwoods less than conifers, perhaps because of less mutual shading of foliage, but differences between tolerance classes are apparent only for the very tolerant hardwoods.

TABLE 8. SHOOT WEIGHT OF SEEDLINGS GROWN IN 13% LIGHT COMPARED WITH THAT OF SEEDLINGS GROWN IN 100% LIGHT FOR TREE SPECIES STUDIED IN THIS SERIES

Tolerance class	Hardwood species	Shoot wt 13% / Shoot wt 100%	Age	Coniferous species	Shoot wt 13% / Shoot wt 100%	Age
Very intolerant				Jack pine	0.02	6
				Larch	0.04	6
Intolerant	White birch	0.38	5	Red pine	0.04	5
Intermediate	Yellow birch	0.38	5	White pine	0.14	5
	White elm	0.19	6			
	White ash	0.66	7			
Tolerant	Silver maple	0.23	5	Black spruce	0.02	9
	Basswood	0.42	6	White spruce	0.15	9
				Eastern white cedar	0.07	9
Very tolerant	Sugar maple	0.52	5	Balsam fir	0.28	9
	Beech	0.65	7	Eastern hemlock	0.48	7

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